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Food, Fuel, and Fire: Assessing the effects of fuel treatments on wildlife habitat quality in longleaf pine-wiregrass ecosystems

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Abstract

Over the past 30 years, the restoration of presumed historical fire regimes on over 3 million ha in the southeastern USA has yielded a landscape dotted with fire-maintained savanna fragments. Within-site studies have shown that fire-maintained savannas contain higher plant diversity than fire-suppressed shrublands, but little is known about their functioning, or whether they will serve as resilient wildlife habitat in the face of future change. Species richness within functional groups is thought to be a primary contributor to ecosystem resilience, because functional redundancy may allow ecological functions to continue being performed even as some species are lost. The purpose of this study was to explore differences in functional group composition on a broad ecoregional sample of fire-maintained savanna fragments. The scope of our study also allowed us to explore regional beta-diversity, which reflects patterns of biodiversity loss and retention at the regional scale and is a critical aspect of conservation, as it can inform the allocation of resources and design of management strategies that best conserve species within large reserve networks. Our focus was on sites with little to no history of anthropogenic disturbance other than fire suppression (e.g. old growth savannas).

We used nested quadrats to sample the understories of 30 frequently-burned savannas in Florida and Georgia, on preserves ranging in size from 50 to 230,000 ha. The understory data were analyzed in conjunction with spatial and site data to identify patterns and relationships among species-level (i.e. functional type), site-level (i.e. fire history), and landscape-level (i.e. preserve size) variables. We conducted nestedness analysis and nonmetric multidimensional scaling in order to assess beta-diversity, and used a generalized linear model in order to identify relationships between functional group richness and site- and landscape-level variables. We found that both functional group richness and overall community composition were highly variable between sites. The between-site compositional dissimilarity we identified using NMDS and PerMANOVA, taken in conjunction with the nested patterns we found in most of the functional group assemblages, suggest a landscape with a high degree of species loss within important functional groups. Using a generalized linear model, we found that significant predictors of functional group richness included site, soil type, average fire interval over 50 years, number of non-fire fuel treatments, and overstory tree density (trees/ha). Longer fire return intervals were associated with lower forb and graminoid species richness on all soil types. While these findings generally support the existing management paradigm, which calls for relatively short fire intervals and lowering overstory density, many differences in functional group richness were not explained by the fire and overstory parameters. Furthermore, the importance of fire and overstory parameters for predicting understory functional group richness varied with the soil type. Restoring fire and overstory structure alone may therefore be insufficient to ensure that ecosystem function and resilience are achieved.

Background and Purpose

More than any other region of the United States, the Southeast exhibits an overlap between fire management and biodiversity conservation priorities. On the order of 6,000 vascular plant taxa occur in the Southeastern Coastal Plain ecoregion, and of these, 1,306 species are endemic, falling just short of the criterion that would qualify the region as one of the Earth's biodiversity hotspots (e.g. 1,500 endemic species) (Myers et al. 2000, Sorrie and Weakley 2001). The majority of these endemics occur in fire-dependent longleaf pine understories, which in turn support one of the largest vertebrate faunas in temperate North America (Sorrie and Weakley 2001, Means 2006). Recognizing the intersection between fire management and wildlife management in the Southeast, the National Cohesive Wildland Fire Management Strategy/Southeast Regional Action Plan calls for overlap with the State Wildlife Action Plans wherever possible, in order to maximize return on investment for public and private landowners alike (NCWFMS/SRAP 2013). Florida's State Wildlife Action Plan identifies one hundred and forty-two Species of Greatest Conservation Need (including several Threatened and Endangered species) associated with frequently-burned longleaf pine understories, and lists fire suppression as one of the top four statewide threats to biodiversity (FL SWAP 2012). Restoring the historical fire regime to longleaf pine-wiregrass systems is therefore not only a matter of national interest, but one of importance in the global biodiversity crisis.

Over the past 30 years, the restoration of presumed historical fire regimes on over 3 million ha in the southeastern USA has yielded a landscape dotted with fire-maintained savanna fragments. Within-site studies have shown that fire-maintained savannas contain higher plant diversity than fire-suppressed shrublands (e.g. Provencher et al. 2001), but little is known about their functioning, and whether they will be resilient in the face of future change. Although the effectiveness of fuel treatments for changing understory structural parameters (i.e. decreased woody cover and increased herbaceous cover/diversity) have been documented by several researchers in longleaf pine systems, it appears that certain plant functional groups important to wildlife may be chronically underrepresented on restored sites (Provencher et al 2001, Kirkman et al. 2004, Kreye et al. 2013). For example, legumes are of particular importance to wildlife both directly (as a protein-rich food source) and indirectly (by replacing N lost to volatilization by fire), but they are among the functional groups that may be depauperate on restored sites (Mehlman 1992, Hendricks and Boring 1999, Provencher et al. 2001, Kirkman et al. 2004). Few studies have isolated and examined the functional group composition of restored longleaf pine understories, and those that have addressed these parameters have been experimental studies at a single location (Provencher et al. 2001, Kirkman et al. 2004, Glitzenstein et al. 2012).

An understanding of functional group composition on fuels-treated longleaf pine savannas is essential to our ability to maintain resilient wildlife habitat in the years ahead. The richness of species within functional groups is thought to be a primary contributor to ecosystem resilience, because when functional redundancy is high, ecological functions may continue to be performed even as some species are lost. The primary objective of this project was to assess the degree to which fuel treatments in longleaf pine savannas are fostering vegetative communities that exhibit resilience within functional groups important to wildlife. The design of our project also allowed us to address a secondary objective, which was the assessment of plant beta-diversity (the component of regional diversity that accumulates due to inter-site differences) through nestedness analysis and nonmetric multidimensional scaling. Beta-diversity reflects patterns of biodiversity loss and retention at the regional scale and is a critical aspect of conservation, as it can inform the allocation of resources and design of management strategies that best conserve species within large reserve networks (Socolar et al. 2016). We gathered data at three scales: landscape-level, site-level, and species-level, and used a variety of analytical tools to explore drivers of functional group composition and beta diversity on a broad ecoregional sample of fire-maintained savanna fragments.

Study Description and Location

Study Sites: Our focus was on sites with little history of anthropogenic disturbance other than fire suppression, since agricultural legacies are known to be associated with novel communities in longleaf pine systems (Hedman et al. 2000, Kirkman et al. 2004, Glitzenstein et al. 2012, Brudvig et al. 2013). We used nested quadrats to sample the understories of 30 frequently-burned savannas in Florida and Georgia, on preserves ranging in size from 50 to 230,000 ha (Figures 1-2, Table 1). Sites included in the study met the following criteria:
  1) No history of intensive agriculture or forestry. This was determined through communication with managing agencies, historical aerial photos, and the presence of old growth indicator species sensitive to soil disturbance (primarily wiregrass, *Aristida stricta*).
  2) At least three documented fuel treatments (the only exception to this criterion was Osceola National Forest, which was later determined to have had only two treatments on record).

The study sites were stratified into three soil types, all of which are common in longleaf pine systems:

        Spodosols (mesic/wet sands, known regionally as flatwoods) – 12 sites

        Entisols (xeric sands, known regionally as sandhills) – 12 sites

        Ultisols (mesic sandy loams, known regionally as clayhills) – 6 sites

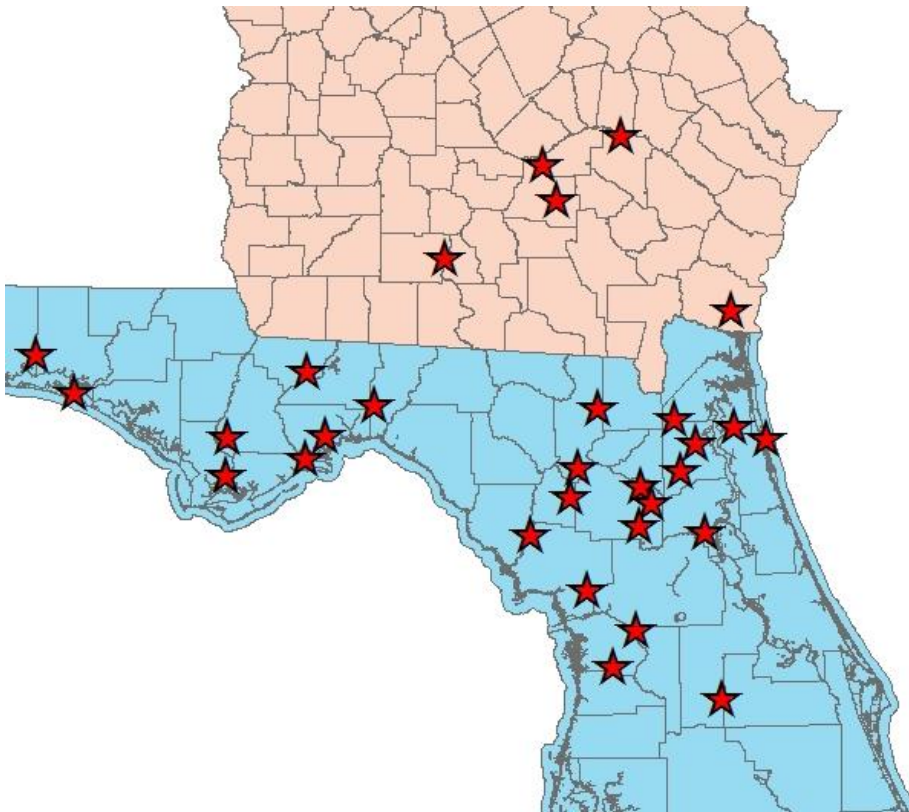**Figure 1**. Study site locations in Florida and Georgia.

Table 1. Study sites with soil type, preserve size, and basic fuel treatment history.

Site	Soil Type	Fuel Treatments	Total # Treatments	Yrs in Fire Rotation	Preserve size (ha)
Austin Cary Memorial Forest	Mesic/Wet Spodosol	Fire Only	5	16	2,148
Apalachicola National Forest	Mesic Ultisol	Fire Only	6	16	567,798
Apalachicola Wildlife Env. Area	Mesic/Wet Spodosol	Fire + Mechanical	8	14	64,471
Aucilla Wildlife Mgmt Area	Mesic/Wet Spodosol	Fire + Chemical	7	14	46,261
Bell Ridge Wildlife Env. Area	Xeric Entisol	Fire + Mechanical	36	49	718
Black Creek Ravines Preserve	Xeric Entisol	Fire Only	7	16	970
Broxton Rocks Preserve	Mesic Ultisol	Fire Only	11	20	1,463
Caravelle Wildlife Mgmt Area	Mesic/Wet Spodosol	Fire + Mechanical	5	16	10,440
Crooked River State Park	Mesic/Wet Spodosol	Fire + Chemical	4	17	511
Eglin Air Force Base	Xeric Entisol	Fire + Chemical	7	17	463,448
General Coffee State Park	Xeric Entisol	Fire + Mechanical	4	9	1454
Goethe State Forest	Mesic/Wet Spodosol	Fire Only	6	21	53,019
Gold Head Branch State Park	Xeric Entisol	Fire Only	10	28	2,366
Guana River Wildlife Mgmt Area	Mesic/Wet Spodosol	Fire + Mechanical	9	12	9,815
Half Moon Wildlife Mgmt Area	Mesic/Wet Spodosol	Fire + Mechanical	4	14	9,554
Jennings State Forest	Mesic/Wet Spodosol	Fire Only	7	22	25,192
Joe Budd Wildlife Mgmt Area	Mesic Ultisol	Fire Only	14	28	1,855
Julington Durbin Preserve	Xeric Entisol	Fire + Chemical	6	10	2,062
Longleaf Flatwoods Preserve	Xeric Entisol	Fire + Mechanical	3	7	2,822
Manatee Springs State Park	Mesic Ultisol	Fire + Mechanical	10	22	2,448
Moody Forest Preserve	Mesic Ultisol	Fire + Mechanical	6	11	4,478
Newnans Lake Preserve	Mesic/Wet Spodosol	Fire Only	4	11	7,537
Ochlockonee River State Park	Mesic/Wet Spodosol	Fire Only	16	39	538
Osceola National Forest	Mesic/Wet Spodosol	Fire + Mechanical	2	6	230,638
Point Washington State Forest	Xeric Entisol	Fire + Chemical	5	18	15,407
Reed Bingham State Park	Xeric Entisol	Fire Only	7	19	1,620
River Rise State Park	Mesic Ultisol	Fire + Mechanical	7	27	4,482
Seminole State Forest	Xeric Entisol	Fire + Mechanical	4	11	123
St. Marks Nat'l Wildlife Refuge	Xeric Entisol	Fire Only	17	49	71,571
Withlacoochee State Forest	Xeric Entisol	Fire Only	10	19	159,625

Figure 2. Sampling a mesic/wet longleaf pine savanna at Caravelle Ranch WMA.

Methods

Site-level parameters: The study sites were sampled using a nested quadrat sampling design, a modified version of the methods of Peet et al. (1998) and Kirkman et al. (2007). At each study site, 5 randomly placed 10m x 10m (100m2) species-area sampling modules were established. Nested in one corner of each $100m^2$ module were $10m^2$, $1m^2$, and $0.1m^2$ quadrats. Understory species presence/absence was recorded in all quadrats, and percent cover to the nearest 5% was recorded in the two smallest quadrats. Overstory tree data was collected in the northwest corner of each $100m^2$ module using the Point-Centered Quarter Method, from which tree density was then calculated. Field data collection occurred primarily during fall 2014 and fall 2015, with some additional botanical data collected through summer 2016. Historical data for each sampling site was collected via a questionnaire distributed to the relevant personnel associated with each site. The questionnaire was created in Adobe Acrobat Pro and contained drop-down and fill-in fields, in which agency personnel entered the dates/descriptions of all known fires, other fuel treatments, and any other management actions known to have occurred on the study sites. We created exact sampling location maps to accompany the questionnaire for each study site, to ensure that information regarding fires and other treatments was as precise as possible. All completed questionnaires were returned to us by June 2016.

Figure 3. Distribution of fire rotation histories across study sites. Active fire rotation is defined as the most recent continuous period of fire with no gaps > 10 years.

From the fire history questionnaires, we developed a variety of quantitative fuel treatment history parameters, based on histories dating back to 1965 (50 years): total number of fires, total number of non-fire fuel treatments, average fire interval over the past 50 years, number of years in active fire rotation (most recent continuous period of fire with no gaps > 10 years), and number of growing season fires. Figure 3 shows the distribution of continuous fire histories across all study sites. The majority of study sites had been in active rotation between 10 and 25 years; three sites had much longer periods of active rotation (35-50 years). This distribution is indicative of the region's overall prescribed fire history; most agencies began using prescribed fire in earnest following the passage of Florida's 1990 Prescribed Burning Act (Brenner & Wade 2003), and our search for study sites turned up a great many that had been put into rotation between the early 1990s and late 2000s.

Landscape-level parameters: We collected landscape-level data using the open access Florida Geographic Data Library and Georgia GIS Clearinghouse (FGDL 2016, GGISC 2016), and derived the relevant parameters in ArcMap 10.3 (ESRI 2015). For each study site, we calculated total preserve area and land use composition of the surrounding land use matrix within a 10km buffer. For the Florida sites, we used the most recent Florida Land Use and Cover vector shapefiles developed by the Florida Department of Environmental Protection, which delineate plant communities and land uses based on True Color photography within each of Florida's five Water Management District regions (FGDL metadata explorer 2016). These shapefiles classify plant communities and land uses according to the Florida Land Use Cover Class System (FLUCCS), which is a three-tiered classification system that includes specific habitat types (i.e. hydric pine savanna, xeric pine-oak woodland, etc.) (FGDL 2016). Within ArcGIS, we calculated the area within each 10km buffer belonging to vegetation types the same as or similar to those under study. For the Georgia sites, we used the Georgia Land Use Trends (GLUT) 2008 Land Use Cover raster dataset to calculate buffer composition. The GLUT land cover categories are broader than the FLUCCS categories (i.e. evergreen forest vs. deciduous forest), but allowed us to roughly calculate the area of each buffer in similar vegetation types.
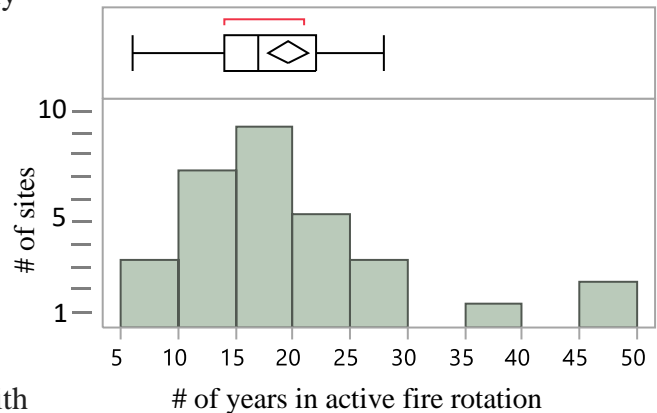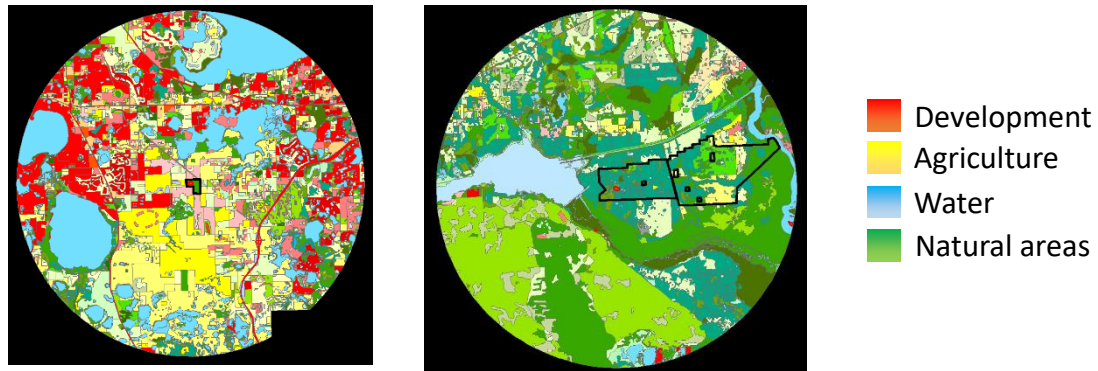
Figure 4. Example of two land use buffers created in ArcGIS. The site on the left (Seminole State Forest) is in a heavily developed and farmed area, and the site on the right (Caravelle Ranch WMA) is adjacent to a number of large protected areas.

Species-level parameters: At the species level, we classified all understory species by functional group (C_4 graminoid, C_3 graminoid, forb, legume, shrub, tree) and seed dispersal type. C_4 and C_3 graminoid classifications followed Waller & Lewis (1979), Barkworth et al. (2003), and Bruhl & Wilson (2007). We classified seeds into dispersal types and associated distance classes following the system developed by Vittoz & Engler (2007): blastochory (creeping stems), boleochory (tiny/light seeds dispersed short distances by wind), ballochory (explosive dehiscence), cystometeochory (balloon-like structures), chamaechory (tumbleweed strategy), pterometeochory (wind dispersal via winged seeds), myrmechory (ant dispersed), trichometeochory (wind dispersal via plumes), epizoochory (external adherance to animals), dyszoochory (burial by animals), endozoochory (consumed by animals). Appendix 1 contains a list of all species found in the study with functional group classifications, seed dispersal types, and seed dispersal distance classes.

Analysis: We developed a generalized linear mixed model using PROC GLIMMIX in SAS 9.4 (SAS Institute Inc. 2013) to determine the importance of landscape- and site-level variables for predicting species richness within functional groups. We began with one random predictive factor (site) and 10 fixed factors (soil type, average fire interval over 50 years, years in continuous fire rotation, number of growing season burns, total number of fires, number of nonfire fuel treatments, preserve size, area of 10km matrix buffer in same/similar community, overstory tree density (trees/ha), and percent shrub cover), and dropped variables from the model sequentially until we achieved the best fit. We conducted the same analysis with mean seed dispersal distance class as a response variable.

We analyzed nestedness, a concept used to explore patterns of species composition among isolated habitats such as landscape fragments, using the public domain software NeD (Strona & Fattorini 2014), in order to determine whether low-diversity assemblages contained nested subsets of the species found in high-diversity assemblages. Nested patterns at the landscape level may indicate a variety of underlying site and species gradients. We created nestedness matrices for each functional group x soil type combination, and used BR (Brualdi and Sandson discrepancy) and NODF (nestedness based on overlap and decreasing fills) indices tested against a CE (proportional row and column total) null model to determine whether the matrices were significantly nested (Strona & Fattorini 2014).

Community composition was analyzed in PC-ORD version 5 (McCune and Mefford 2006), using nonmetric multidimensional scaling (NMS), which is recommended for ordination of most types of plant community data (McCune and Grace 2002). We conducted the NMS ordination using a Sørenson distance measure (Sørenson 1948) to maximize sensitivity and minimize error at moderate and large distances (McCune and Grace 2002). Data were square root–transformed to reduce stress. PC-ORD conducted 250 runs with real data and 250 runs with randomized data and selected the lowest-stress (i.e., best fit) solution. Significance of the chosen solution was determined using a Monte Carlo test comparing the real data with the randomized data. Species with fewer than 2 occurrences (which

represented 5% of the sample units in each site type) were dropped from the analysis to reduce the noise effects of rare species (McCune and Grace 2002). We used PerMANOVA to test for significant differences in community composition between sites, with a Benjamini-Hochberg correction to adjust for multiple comparisons.

Key Findings

1. **Between-site differences**: We found pronounced differences in species and functional group richness between sites. Table 2 shows the ranges of values found at each site, broken down by soil type and functional group. The whole-site values in Table 1 represent the cumulative number of species found in all five sampling modules at each site. The most species-rich sites typically contained anywhere from two to five times as many species per functional group as the least species-rich sites. At the 100m^2 sampling module level (Table 3), forb, legume, shrub, tree, and overall species richness varied significantly between sites, while C_4 and C_3 graminoid cover did not vary significantly between sites.

NMS ordination was conducted on the 100m^2 quadrat data within each soil type, and showed very distinct differences in community composition between sites on Entisols and Ultisols (Figures 5-6). Spodosol sites exhibited less separation between sites on the ordination axes (Figure 7). Three-dimensional NMS solutions were chosen for all three soil types, with a final stress of 19.4 for the Entisol plot, 14.0 for the Spodosol plot, and 12.3 for the Ultisol plot. PerMANOVA applied to the Sorensen distance matrix showed that overall community composition varied significantly by site on all three soil types (Table 4), and associated pairwise

Table 2. Whole site species richness

	Range	Mean
Entisols (n=12)		
C3 graminoids	1 – 5	3
C4 graminoids	8 – 19	14
Forbs	14 – 32	24
Legumes	1 – 14	10
Shrubs	5 – 16	9
Trees	3 – 12	6
All species	45 – 88	68
Spodosols (n=12)		
C3 graminoids	2 – 9	4
C4 graminoids	5 – 16	10
Forbs	10 – 49	20
Legumes	0 – 4	1
Shrubs	12 – 21	16
Trees	1 – 6	4
All species	36 – 93	58
Ultisols (n=6)		
C3 graminoids	4 – 6	5
C4 graminoids	8 – 20	15
Forbs	9 – 48	36
Legumes	6 – 12	9
Shrubs	11 – 24	16
Trees	4 – 15	9
All species	62 – 112	94

comparisons were significant for all but one pair of sites following a Benjamini-Hochberg correction. This high degree of dissimilarity may or may not be associated with high beta-diversity, depending on whether the sites exhibit nestedness (some sites contain smaller subsets of the species on other sites) or species turnover (species found at some sites are replaced by different species at other sites) (Socolar et al. 2016).

Table 3. Species richness comparisons at the 100m^2 quadrat level based on a generalized linear mixed model.

	Species Richness (100m^2)						
	p > |t|						
	C3 graminoids	C4 graminoids	Forbs	Legumes	Shrubs	Trees	All Species
Soil	0.0778	0.1829	0.4077	**0.0037**	0.6241	**0.0022**	0.1287
Fire Interval	0.7244	0.3653	0.4130	0.9643	**0.0187**	0.7919	0.3320
Fire Interval x Soil	**0.0214**	**0.0243**	0.0231	0.4098	**0.0177**	0.1492	0.0531
Other Treatments	0.2445	0.6648	**0.0134**	0.2528	0.1099	0.4120	0.4301
Other Trtmts x Soil	0.5114	0.1070	**0.0203**	0.7980	**0.0089**	0.1033	0.1305
Overstory Density	0.8072	0.9596	0.1476	0.8813	0.8182	0.8911	0.6814
Overstory Density x Soil	0.1679	0.3774	**0.0469**	**0.0426**	0.0980	0.8316	**0.0246**
	p > χ^2						
Site covariance	0.2619	0.1492	**<.0001**	**<.0001**	**.0313**	**.0016**	**<.0001**

Figure 5. Nonmetric multidimensional scaling (NMS) ordination of understory community composition on Entisol sites, viewed on axes 1 and 3 of the three-dimensional NMS model.

Figure 6. Nonmetric multidimensional scaling (NMS) ordination of understory community composition on Ultisol sites, viewed on axes 1 and 3 of the three-dimensional NMS model.
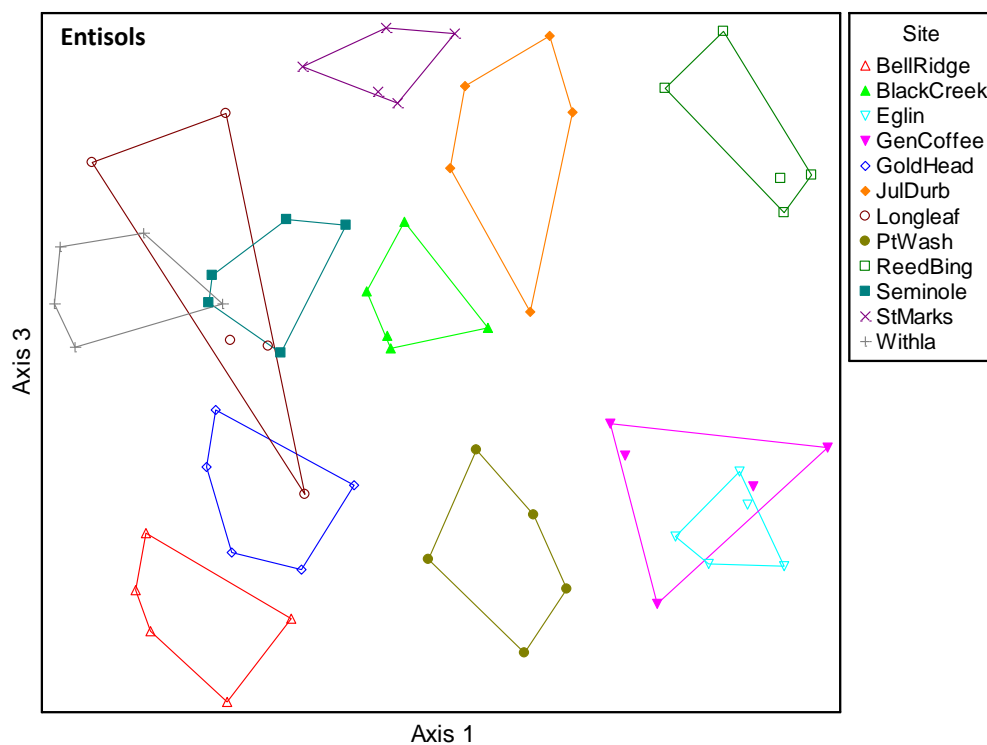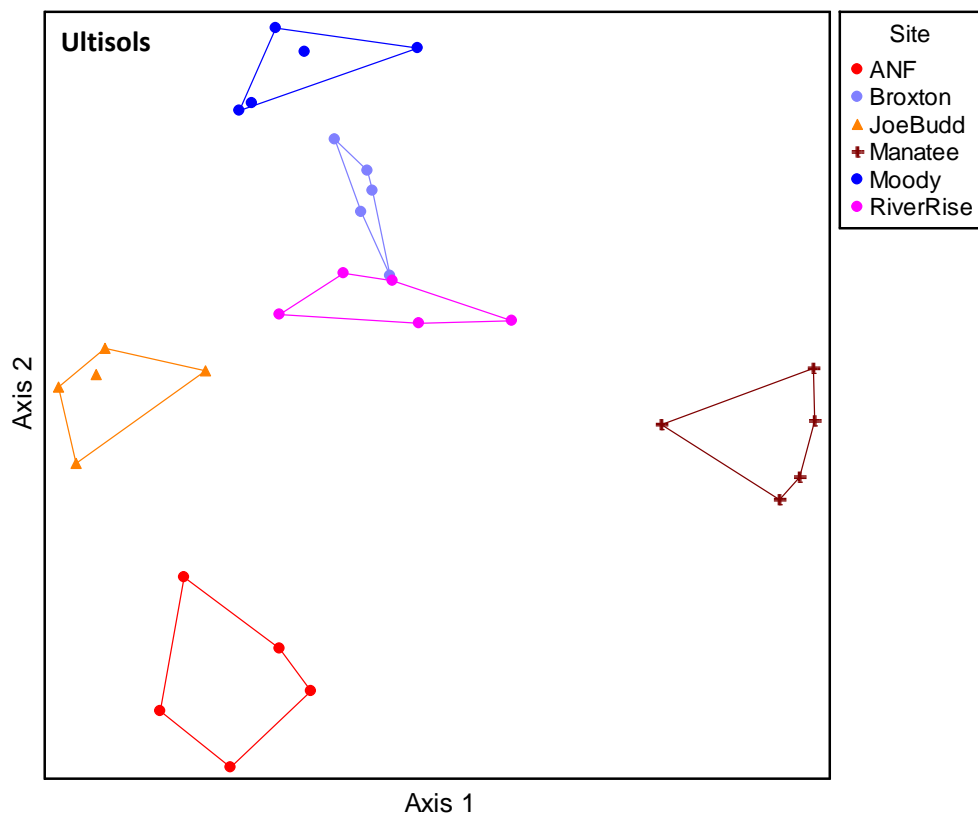
Figure 7. Nonmetric multidimensional scaling (NMS) ordination of understory community composition on Spodosol sites, viewed on axes 1 and 3 of the three-dimensional NMS model.
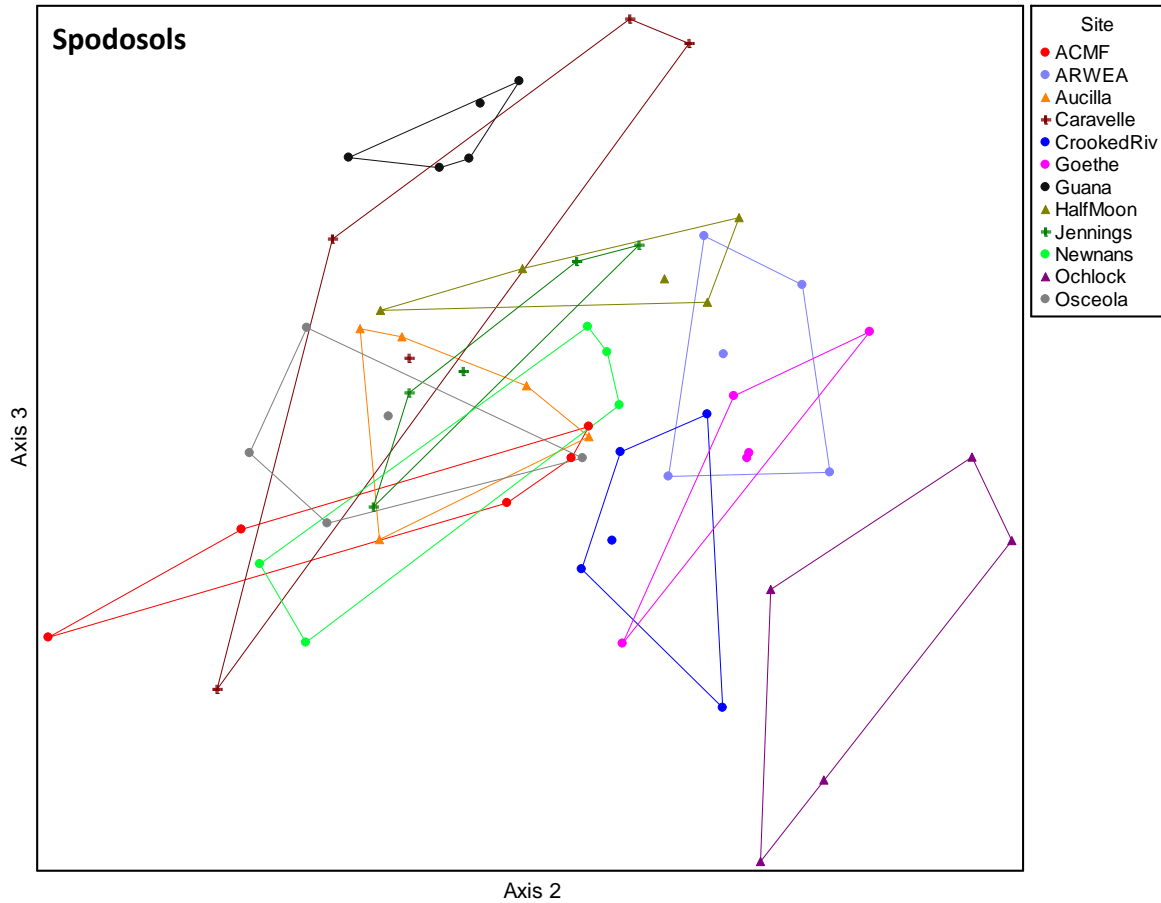

Table 4. PerMANOVA comparison of community composition in 100 m^2 quadrats. Quadrat similarity is based on a Sorensen distance measure.

	d.f.	SS	MS	F	p*
Entisols					
Site	11	10.778	0.97978	9.1799	0.0002
Residual	48	5.1231	0.10673		
Total	59	15.901			
Spodosols					
Site	11	10.396	0.94513	7.3359	0.0002
Residual	48	6.1841	0.12884		
Total	59	16.581			
Ultisols					
Site	5	5.0901	1.0180	7.2169	0.0002
Residual	24	3.3854	0.14106		
Total	29	8.4755			

2. **Predictive variables**: The best-fit generalized linear model contained five of our original eleven site- and landscape-level variables. Significant predictors of functional group richness included: site, soil type, average fire interval over 50 years ("Fire Interval"), number of non-fire fuel treatments ("Other Treatments"), and overstory tree density (trees/ha) ("Tree Density") (Table 3). There were numerous soil interactions, which are delineated in Table 5. Longer fire return intervals were associated

with lower forb and graminoid species richness on all soil types, especially at the 10m^2 and 100m^2 scales. The number of nonfire fuel treatments was positively associated with shrub and tree species richness on Entisols; the reason for this is not clear, but it is possibly an artifact of the study design—sites with higher levels of woody encroachment are simply more likely to have had additional hardwood removal interventions, and may have had higher levels of shrub species richness to begin with. Forb richness and overall richness were higher on Spodosol sites with nonfire fuel treatments. On Ultisols, C$_3$ graminoid richness was positively associated with nonfire treatments, whereas forb richness was negatively associated with nonfire treatments; this again may be an artifact of more fire-suppressed sites having had more treatments. Overstory tree density was negatively associated with legume richness on Entisols and with forb, legume, shrub, tree, and overall species richness on Spodosols, but was positively associated with legume and shrub richness on Ultisols.

Table 5. Generalized linear mixed model results for functional group richness within soil types at all scales of measurement. The sign in parentheses shows the direction of the relationship.

Species Richness	Avg fire return interval			# of nonfire fuel treatments			Overstory density (trees/ha)		
	1m^2	10m^2	100m^2	1m^2	10m^2	100m^2	1m^2	10m^2	100m^2
Entisols	p > |t|	p > |t|	p > |t|	p > |t|	p > |t|	p > |t|	p > |t|	p > |t|	p > |t|
C3 graminoid		0.014 (-)							
C4 graminoid									
Forb		0.016 (-)	0.024 (-)						
Legume									0.050 (-)
Shrub						0.016 (+)			
Tree						0.015 (+)			
All species		0.018 (-)	0.016 (-)						
Spodosols									
C3 graminoid		0.044 (-)							
C4 graminoid	0.003 (-)		0.007 (-)						
Forb		0.005 (-)	0.009 (-)		0.034 (+)	0.006 (+)			0.014 (-)
Legume									0.027 (-)
Shrub									0.010 (-)
Tree									0.029 (-)
All species						0.045 (+)			0.007 (-)
Ultisols									
C3 graminoid					0.020 (+)	0.011 (+)			
C4 graminoid		0.032 (+)							
Forb						0.003 (-)			
Legume									0.023 (+)
Shrub									0.034 (+)
Tree									
All species									

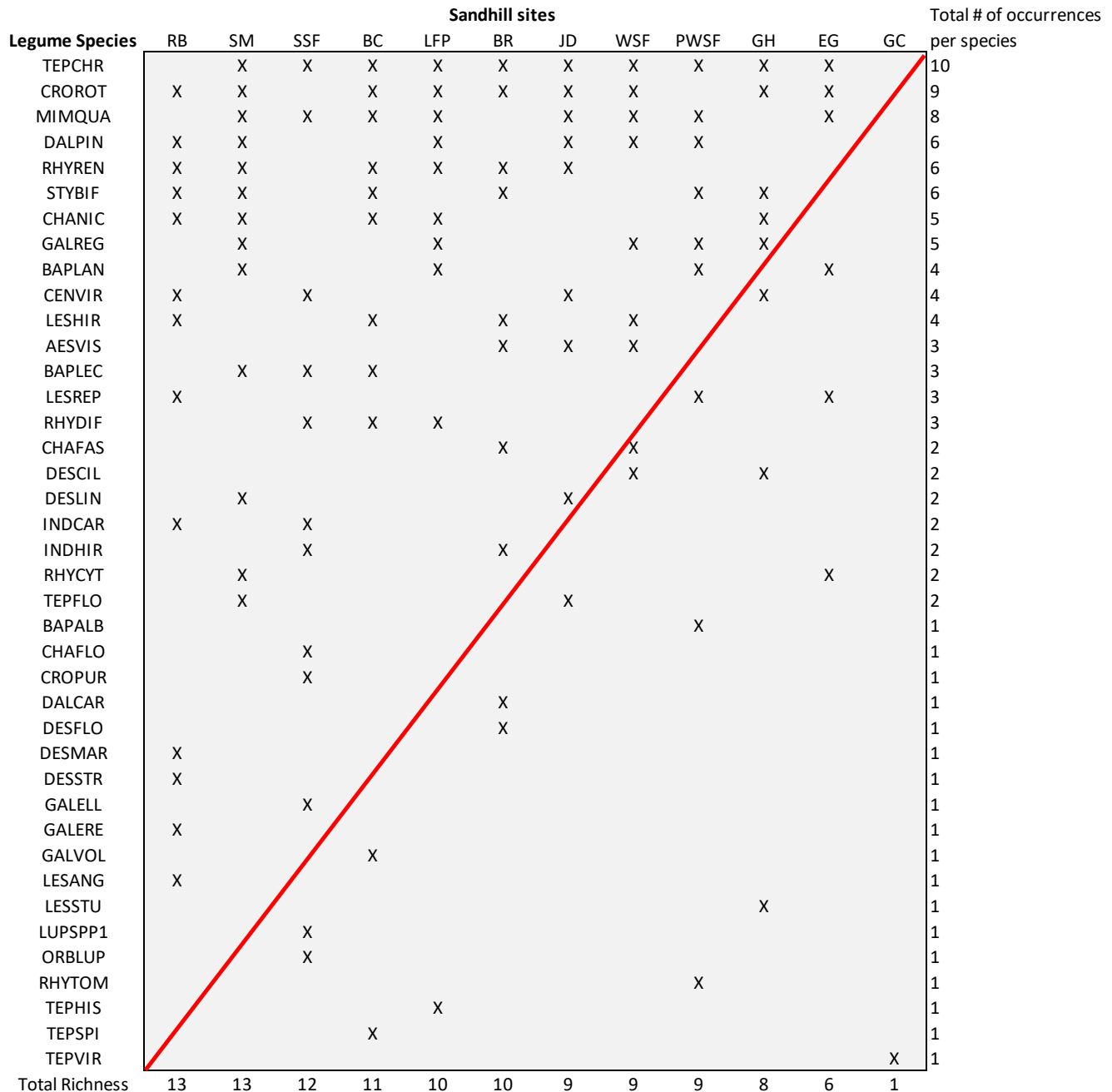2. **Species-level analysis**:

Nestedness analysis showed that species assemblages were significantly nested for many of the functional group/soil type combinations (Table 6). Forb, C4 graminoid, and shrub assemblages were nested on all soil types, while legume and tree assemblages were nested only on Entisols and C3 graminoid assemblages were nested only on Spodosols. The nested patterns found in many functional group x soil combinations suggests that species assemblages on less diverse sites are subsets of those found on more diverse sites. These patterns may be caused by environmental gradients, species characteristics, or mass effects (a hypothesized facet of metacommunities in which species present in more patches have higher colonization potential, and are able to repeatedly repopulate patches where

they are extirpated). Nestedness is negatively related to beta diversity (the cumulative diversity of local species assemblages), because species present at one site are absent at another, but are not replaced by additional species (Socolar et al. 2016). The high degree of nestedness we found in our sample therefore suggests low beta diversity, despite the high degree of dissimilarity between sites. The presence of nested patterns in our study system also suggests that they are dominated by extinction rather than immigration (Wright & Reeves 1992). However, seed dispersal distance class did not vary significantly between sites, and was not predicted by any of our site- and landscape-level parameters. This result suggests that factors other than seed dispersal may be more important for predicting species presence/absence on formerly fire-suppressed sites. Other species-level factors that could predict persistence on longleaf pine savanna remnants might include extinction-related paramters such as seed bank longevity, shade tolerance, and early competitive ability.

Table 6. Nestedness analysis of species composition within soil types and functional groups.

Entisols	Index	Z-score	RN	Nested?	
C3 graminoids	33.773	1.405	0.2	No	$p > 0.05$
C4 graminoids	41.845	4.886	0.22	Yes	**$p < 0.001$**
Forbs	30.898	5.551	0.164	Yes	**$p < 0.001$**
Legumes	0.313	2.275	0.153	Yes	**$p < 0.05$**
Shrubs	34.021	3.911	0.206	Yes	**$p < 0.001$**
Trees	71.655	6.472	0.465	Yes	**$p < 0.001$**
Spodosols					
C3 graminoids	39.206	3.19	0.352	Yes	**$p < 0.001$**
C4 graminoids	35.826	3.069	0.199	Yes	**$p < 0.01$**
Forbs	27.276	5.53	0.262	Yes	**$p < 0.001$**
Legumes	23.38	0.397	0.088	No	$p > 0.05$
Shrubs	48.149	4.028	0.164	Yes	**$p < 0.001$**
Trees	18.847	-0.842	-0.124	No	$p > 0.05$
Ultisols					
C3 graminoids	23.125	-0.612	-0.075	No	$p > 0.05$
C4 graminoids	39.547	2.28	0.127	Yes	**$p < 0.05$**
Forbs	33.467	4.01	0.102	Yes	**$p < 0.001$**
Legumes	27.988	-0.329	-0.025	No	$p > 0.05$
Shrubs	41.234	2.702	0.158	Yes	**$p < 0.01$**
Trees	41.884	0.349	0.035	No	$p > 0.05$

Figure 8. Nestedness matrix for sandhill legume assemblages. Sites are in columns, ordered left to right from most species-rich to least species-rich. Species are in rows, ordered top to bottom from most common to least common. In a perfectly nested matrix, all species occurrences would occur above the red line.

Legume Species	RB	SM	SSF	BC	LFP	BR	JD	WSF	PWSF	GH	EG	GC	Total # of occurrences per species
TEPCHR		X	X	X	X	X	X	X	X	X	X		10
CROROT	X	X		X	X	X	X	X		X	X		9
MIMQUA		X	X	X	X		X	X	X		X		8
DALPIN	X	X			X		X	X	X				6
RHYREN	X	X		X	X	X	X						6
STYBIF	X	X		X		X			X	X			6
CHANIC	X	X		X	X					X			5
GALREG		X			X			X	X	X			5
BAPLAN		X			X				X		X		4
CENVIR	X		X				X			X			4
LESHIR	X			X		X		X					4
AESVIS						X	X	X					3
BAPLEC		X	X	X									3
LESREP	X								X		X		3
RHYDIF			X	X	X								3
CHAFAS						X		X					2
DESCIL								X		X			2
DESLIN		X					X						2
INDCAR	X		X										2
INDHIR			X			X							2
RHYCYT		X									X		2
TEPFLO		X					X						2
BAPALB									X				1
CHAFLO			X										1
CROPUR			X										1
DALCAR						X							1
DESFLO						X							1
DESMAR	X												1
DESSTR	X												1
GALELL			X										1
GALERE	X												1
GALVOL				X									1
LESANG	X												1
LESSTU										X			1
LUPSPP1			X										1
ORBLUP			X										1
RHYTOM									X				1
TEPHIS					X								1
TEPSPI				X									1
TEPVIR												X	1
Total Richness	13	13	12	11	10	10	9	9	9	8	6	1	

Management Implications

The between-site compositional dissimilarity we identified using NMDS and PerMANOVA, taken in conjunction with the nested patterns we found in most of the functional group assemblages, suggests a landscape with a high degree of species loss within important functional groups. In reserve systems with nested assemblages, it has been suggested that: 1) conservation should prioritize the richest sites rather than spreading resources among many sites without regard to their richness (Socolar et al. 2016), and 2) conservation managers should seek to minimize nestedness in systems of nature reserves, because of the negative relationship between nestedness and beta diversity (Wright & Reeves 1992). In the longleaf pine savanna region, minimizing nestedness might entail species reintroductions as well as

tailoring fire regimes to the specifics of each site, in order to enhance survival and reproduction within key functional groups.

Variation between sites of the same community type is to be expected in any plant community, due to myriad biotic, abiotic, and historical factors that vary from site to site. In a management context, the importance of the observed between-site variation is that longleaf pine savanna sites are currently evaluated for quality by managing agencies based largely on non-site-specific structural parameters. These parameters include native bunchgrass dominance in the understory and a low basal area pine overstory, both of which are maintained by a prescribed 1-3 year early growing season fire return interval. The management of these sites follows an ecological restoration framework, using historical reference templates for identifying both fire-return intervals and target vegetation parameters. However, our research shows that sites vary greatly in their functional group richness and composition—and therefore their resilience—despite their overall community similarity. A one-size-fits-all management approach that focuses solely on structural parameters may therefore be detrimental to functional group resilience. For example, a site low in legume species richness may benefit from varying the season of burn and the fire return interval (Hiers et al. 2000) rather than implementing solely early growing season burns on a fixed return interval, as is common practice among managing agencies in the Southeast.

Our data showed that site-to-site differences in functional richness can be partially attributed to the long term fire history, overstory tree density, and number of mechanical/chemical fuel treatments applied to a site (all variables that are likely interrelated). While these findings generally support the existing management paradigm, which calls for relatively short fire intervals and lowering overstory density, many differences in functional group richness were not explained by the fire and overstory parameters. Furthermore, the importance of fire and overstory parameters for predicting understory functional group richness varied with the soil type. Restoring fire and overstory structure alone may therefore be insufficient to ensure that ecosystem function and resilience are achieved. Site-specific management should therefore begin with a species-level plant and animal survey to provide baseline data, and fire prescriptions should be based on the species and functional group composition present on an individual site. At the regional level, beta-diversity will benefit most from the prioritization of the richest sites rather than restoration of degraded sites.

Relationship to other recent findings

Since the majority of remnant longleaf pine savanna sites have been degraded by agriculture or forestry, many recent plant diversity studies within the region have focused on comparisons of old growth sites to disturbed sites, such as old fields and former plantations. These studies have shown that altered species compositions (higher proportions of ruderal species and the absence of many characteristic species) are evident as long as half a century after abandonment (Hedman et al. 2000, Kirkman et al. 2004, Glitzenstein et al. 2012, Brudvig et al. 2013), and that dispersal limitation is likely the predominant factor affecting native re-colonization of former agricultural land (Kirkman et al. 2004, Ostertag and Robertson 2007, Brudvig et al. 2013). Decreased soil water holding capacity in post-agricultural longleaf pine woodland soils may also play a role in observed compositional differences, but evidence has not been found that other long-term abiotic soil changes affect recolonization potential in these systems (Brudvig et al. 2013). Our finding that the proportion of different seed dispersal mechanisms (and their associated distance classes) were not significantly related to fire or management history contrasts with the aforementioned studies, which is likely due in part to the fact that all of our study sites can essentially be considered old growth grasslands (Veldman et al. 2015). Unlike the studies that included agriculturally-impacted sites, our study sites contained a very low proportion of ruderal species, which often exhibit long-distance dispersal mechanisms and dominate former agricultural sites (Vellend et al. 2007). If we had included sites with agriculture and forestry legacies in our study, our beta-diversity metrics might reflect species turnover rather than nestedness, due to the replacement of old growth species by ruderal species (Socolar et al. 2016). However, given the long-

term imprint of agriculture and forestry on longleaf pine savanna understories, sites with more severe disturbance histories may represent novel communities and should probably be considered separately from relatively undisturbed savanna fragments in the assessment of beta diversity.

Another area of recent research in longleaf pine savannas concerns the impacts of very short (1-3 year) fire rotations on mast production and vertebrate diversity. Historical documents, in conjunction with the life-history traits of dominant species and endangered grassland specialists, have provided the bulk of the evidence for a consensus that the historical reference community for most uplands in the region is a structurally homogenous, bi-layered savanna with a grass-dominated herbaceous understory and a near-monotypic longleaf pine overstory (Chapman 1932; Frost 1998; Gilliam & Platt 1999; Shappell and Koontz 2015). These conditions can only be maintained by very frequent fire (every 1-3 years); however, recent research has revealed conflicts with plant and animal species that are also native components of the ecosystem but survive and reproduce best under somewhat longer intervals (i.e. every 3-5 years) and more heterogeneous vegetation conditions (Hiers et al. 2014, Lashley et al. 2015, Darracq et al. 2016). In particular, many researchers have expressed concern that adherence to a narrowly defined fire rotation overlooks the critical wildlife habitat role of the mast-producing shrub species that are also native to longleaf pine savannas, most of which require at least 3-5 year inter-fire intervals in order to produce mast (Perkins et al. 2008; Hiers et al. 2014, Lashley et al. 2015, Darracq et al. 2016). These studies complement our findings, in that they focus on functional group responses to different fire regimes, and suggest that the prevailing management recommendations for longleaf pine systems are oversimplified and may be detrimental to the conservation of site-specific and region-wide biodiversity.

A third area of recent research relevant to our study relates to the impacts of shrub and tree encroachment in savanna and grassland communities. A pervasive assumption in both the scientific and policy literature is that fire suppression causes the degradation of biotic communities and ecosystem processes, primarily via the encroachment of woody species into historically herbaceous-dominated or mixed shrub-herbaceous communities (Ratajczak et al. 2012). Many prescribed fire programs worldwide, including those used to manage longleaf pine savannas, are aimed at reversing, preventing, or managing woody encroachment due to fire suppression. The consistency with which fire suppression and attendant woody encroachment result in ecological degradation, however, is a much more complex issue than is usually acknowledged. A recent meta-analysis of 244 woody encroachment studies worldwide found no consistent relationship between woody encroachment and ecosystem structure/functioning variables; rather, response variables were equally likely to have positive, neutral, or negative directions associated with woody encroachment; and species richness in particular had neutral to positive responses (Eldridge et al. 2011). Other recent studies have suggested that ecosystem functions and plant diversity are maximized when intermediate levels of woody plant cover are present (Soliveres et al. 2014; Eldridge & Soliveres 2015; Barbosa de Silva et al. 2016). Ratajczak et al. (2012), in a meta-analysis of 29 North American grassland and savanna studies, found that the strength and direction of the effects of woody encroachment depends heavily on climatic variables, with communities in wetter climates experiencing stronger encroachment-related declines in species richness than those in drier climates (Ratajczak et al. 2012). This conclusion is in line with our finding that overstory tree density was related to total species richness in longleaf pine communities occuring on poorly drained Spodosols, but not on excessively drained Entisols or well drained Ultisols.

Future Work Need

Our results showed that the relationship between fuel treatment history and understory functional group richness varied greatly by functional group and soil type. A substantial component of variation in functional richness was unexplained by fire and fuel treatment history, indicating that the restoration of vegetation structure according to historical reference templates alone may not produce resilient plant communities. In other cases where empirical studies have looked at specific fire regime-related ecological parameters independent of accepted reference system templates, they have often produced

results that run counter to reference system-based recommendations for the same system (e.g. small mammals in ponderosa pine forests: Converse et al. 2006; mast consumption in longleaf pine savannas: Hiers et al. 2014, Lashley et al. 2015; vertebrate diversity in longleaf pine savannas: Darracq et al. 2016; vertebrate diversity in sagebrush steppe: Rowland et al. 2006). Studies such as these point to the need for an expanded conceptual framework to guide managed fire regimes in longleaf pine savannas—one that draws from a historical narrative as a starting point, but moves beyond it toward a more flexible and ecologically nuanced approach to prescribed fire.

Several recent reviews have suggested that research in support of managed fire regimes should emphasize a deeper understanding of fire-biota interactions across trophic levels, functional groups, and spatial and temporal scales. Driscoll et al. (2010) identified three broad research areas needed to support fire management for biodiversity conservation: 1) understanding the mechanistic causes of species responses to fire regimes (such as functional traits); 2) studying the ways in which spatial and temporal fire mosaics influence species spread and persistence; and 3) identifying interactions between fire regimes and other processes that can modify species responses (e.g. rainfall, habitat fragmentation). Similarly, Kelly et al. (2016) recommend that fire regime research intended to guide management objectives and actions should emphasize four focus areas: context, mechanisms, functional heterogeneity, and uncertainty. Bowman et al. (2016) propose that the concept of pyrodiversity, defined by them as "the outcome of the trophic interactions and feedbacks between fire regimes, biodiversity, and ecological processes," could serve as a unifying framework for the study of fire/biodiversity relationships. Under this definition, the pyrodiversity concept largely overlaps with the conceptual research frameworks delineated by Driscoll et al. (2010) and Kelly et al. (2016), and all three frameworks offer multi-faceted approaches to elucidating fire-biota relationships in the modern landscape. Future research in longleaf pine savannas should focus on identifying mechanistic relationships between prescribed fire regimes and functional group composition, so that prescribed fire and other associated fuel treatments can be used more effectively to create resilient plant communities.

Deliverables Crosswalk

Proposed	Delivered	Status
Present results at an international scientific research conference.	Oral presentation by Johanna Freeman at Ecological Society of America conference in Ft. Lauderdale, FL, August 2016.	Complete
Present results to the Native Groundcover Steering Committee of the Florida Fish & Wildlife Conservation Commission (FFWCC)	Oral presentation by Johanna Freeman to the FFWCC at the Gainesville, FL Wildlife Research Laboratory, June 2016.	Complete
Plan and present workshop for federal, state, and private land managers and forest owners (with Southern Fire Exchange)	Presentation by Johanna Freeman and field tour by Leda Kobziar at a Southern Fire Exchange workshop entitled: "Connecting Fire Management and Ecosystem Restoration: What about groundcover diversity?" Ordway-Swisher Biological Station, Melrose FL, April 2016.	Complete
Publish results on the FFWCC, UF Fire Science Lab, and Southern Fire Exchange JFSP Regional Consortium websites.	Website content being prepared in consultation with site managers	In preparation

Publish research digest and fact sheet with Southern Fire Exchange	Research digest and fact sheet being prepared in consultation with SFE coordinator.	In preparation
Publish results in Student Investigator's doctoral dissertation	Dissertation in draft form, defense scheduled May 8, 2017.	In preparation
Publish results in peer-reviewed journals	Journal submission expected August 2017.	In preparation
	Additional Deliverables	
	Conference poster: Freeman, J., Kobziar, L. N. 2015. Can we restore resilient savanna plant communities in the modern landscape? Poster, Sixth International Association for Fire Ecology Congress, San Antonio, TX, 16-20 November.	Complete

ESRI. May 2015. ArcGIS 10.3.1.

Barbosa da Silva F.H., Arieira J., Parolin P., Nunes da Cunha C., Junk W.J. 2016. Shrub encroachment influences herbaceous communities in flooded grasslands of a neotropical savanna wetland. Applied Vegetation Science **19**(3): 391-400.

Barkworth M.E., Capels K.M., Long S., Piep M.P. 2003. Flora of North America; north of Mexico. Volume 25, Magnoliophyta: Commelinidae (in part). Poaceae. part 2. New York: Oxford University Press xxv, 783p. - illus..

Brenner, J, and Wade, D. 2003. Florida"s Revised Prescribed Fire Law: Protection For Responsible Burners. Pages 132-136 in K.E.M. Galley, R.C. Klinger, and N.G. Sugihara (eds.). Proceedings of Fire Conference 2000: The First National Congress on Fire Ecology, Prevention, and Management. Miscellaneous Publication No. 13, Tall Timbers Research Station, Tallahassee, FL.

Florida Geographic Data Library. http://www.fgdl.org/metadata/metadata_archive/fgdl_html/sflu95.htm http://www.fgdl.org/metadataexplorer/explorer.jsp

Bruhl, J.J., and K.L. Wilson. 2007. Towards a comprehensive survey of C3 and C4 photosynthetic pathways in Cyperaceae. Aliso: A Journal of Systematic and Evolutionary Botany 23: 99-148.

Chapman H.H. 1932. Is the longleaf type a climax? Ecology **13**(4): 328-334.

Converse S.J., Block W.M., White G.C. 2006. Small mammal population and habitat responses to forest thinning and prescribed fire. Forest ecology and management **228**(1): 263-273.

Darracq A.K., Boone W.W., McCleery R.A. 2016. Burn regime matters: A review of the effects of prescribed fire on vertebrates in the longleaf pine ecosystem. Forest Ecology and Management (378): 214-221.

Dobkin DS, Sauder J.D. 2004. Shrubsteppe landscapes in jeopardy. Distributions, abundances, and the uncertain future of birds and small mammals in the Intermountain West. High Desert Ecological Research Institute, Bend, OR.

Driscoll D.A., Lindenmayer D.B., Bennett A.F., Bode M., Bradstock R.A., Cary G.J., Clarke M.F., Dexter N., Fensham R., Friend G., Gill M. 2010. Fire management for biodiversity conservation: key research questions and our capacity to answer them. Biological conservation **143**(9): 1928-1939.

Eldridge D.J., Soliveres S. 2015. Are shrubs really a sign of declining ecosystem function? Disentangling the myths and truths of woody encroachment in Australia. Australian Journal of Botany 62(7): 594-608.

Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecology Letters **14**(7): 709-722.

Florida Fish and Wildlife Conservation Commission. 2012. Florida's State Wildlife Action Plan: A comprehensive wildlife conservation strategy. http://myfwc.com/conservation/special-initiatives/fwli/action-plan/

Frost C.C. 1998. Presettlement fire frequency regimes of the United States: A first approximation. Fire in ecosystem management: Shifting the paradigm from suppression to prescription, ed. TL Pruden and LA Brennan, 70-81.

Gilliam F.S., Platt W.J. 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth Pinus palustris (longleaf pine) forest. Plant Ecology **140**(1):15-26.

Glitzenstein, J.S., Streng, D.R., Masters, R.E., Robertson, K.M., and S.M. Hermann. 2012. Fire frequency effects on vegetation in north Florida pinelands: Another look at the long-term Stoddard Fire Research Plots at Tall Timbers Research Station. Forest Ecology and Management 264: 197-209.

Hedman, C.W., S.L. Grace, and S.E. King. 2000. Vegetation composition and structure of southern coastal plain pine forests: an ecological comparison. Forest Ecology and Management 134:233-247.

Hendricks, J.J. and L.R. Boring. 1999. N_2 fixation by native herbaceous legumes in burned pine ecosystems of the southeastern United States. *Forest Ecology and Management* 113: 167-177.

Hiers, J. K., Wyatt, R., & Mitchell, R. J. (2000). The effects of fire regime on legume reproduction in longleaf pine savannas: is a season selective?. Oecologia, 125(4), 521-530.

Hiers J.K., Walters J.R., Mitchell R.J., Varner J.M., Conner L.M., Blanc L.A., Stowe J. 2014. Ecological value of retaining pyrophytic oaks in longleaf pine ecosystems. The Journal of Wildlife Management, 78(3): 383-393.

Kelly L.T., Brotons L., McCarthy M.A. 2016. Putting pyrodiversity to work for animal conservation. Conservation Biology. doi:10.1111/cobi.12861.

Kirkman, L. K., K. L. Coffey, R. J. Mitchell, and Moser, E. B. 2004. Ground cover recovery patterns and life-history traits: implications for restoration obstacles and opportunities in a species-rich savanna. *Journal of Ecology* 92: 409-421.

Kirkman, L.K., Mitchell, R.J., Kaeser, M.J., Pecot, S.D. and Coffey, K.L., 2007. The perpetual forest: using undesirable species to bridge restoration. Journal of Applied Ecology, 44(3), pp.604-614.

Kreye, J.K., Kobziar, L.N., and J.M. Camp. 2013. Immediate and short-term response of understory fuels following mechanical mastication in a pine flatwoods site of Florida, USA. Forest Ecology and Management, in press.

Lashley M.A., Chitwood M.C., Harper C.A., DePerno C.S., Moorman C.E. 2015. Variability in fire prescriptions to promote wildlife foods in the longleaf pine ecosystem. Fire Ecology **11**(3): 62-79.

McCune, B., and J. Grace. 2002. Analysis of Ecological Communities. MJM Software Design, Gleneden Beach, Oregon, USA.

McCune, B., and M.J. Mefford. 2006. PC-ORD. Multivariate Analysis of Ecological Data. Version 5. MJM Software, Gleneden Beach, Oregon, USA.

Means, D.B. 2006. Vertebrate faunal diversity of longleaf pine ecosystems. Pages 157-216 in S. Jose, E. Jokela, and D. L. Miller, editors. The longleaf pine ecosystem. Springer Science + Business Media, LLC., New York.

Mehlman, D.W. 1992. Effects of fire on plant community composition of North Florida second growth pineland. Bulletin of the Torrey Botanical Club **119:**376-383.

Myers, R.K., Mittermeier, R.A., Mittermeier, C.G., Da Fosseca, G.A.B., and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853-858.

Ostertag, T.E. and K.M. Robertson. 2007. A comparison of native versus old-field vegetation in upland pinelands managed with frequent fire, South Georgia, USA. In Tall Timbers Fire Ecology Conference Proceedings Vol. 23: 109-120.

Peet, R.K., Wentworth, T.R., and P.S. White. 1998. A flexible multipurpose method for recording vegetation composition and structure. Castanea 63: 262-274.

Perkins M.W., Conner L.M., Howze M.B. 2008. The importance of hardwood trees in the longleaf pine forest ecosystem for Sherman's fox squirrels. Forest Ecology and Management. **255**(5): 1618-1625.

Provencher, L., Herring, B.J., Gordon, D.R., Rogers, H.L., Galley, K.E.M., Tanner, G.W., Hardesty, J.L., and L.A. Brennan. 2001. Effects of hardwood reduction techniques on longleaf pine sandhill vegetation in northwest Florida. Restoration Ecology **9:**13-27.

SAS Institute Inc. 2013. SAS 9.4. Cary, NC, USA.

Ratajczak Z., Nippert J.B., Collins, S.L. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. Ecology **93**(4): 697-703.

Shappell L.J., Koontz S.M. 2015. Fire reintroduction increased longleaf pine (Pinus palustris L.) recruitment and shifted pine demographics in a long-unburned xeric sandhill assemblage. Forest Ecology and Management **354**: 344-352.

Socolar, J.B., Gilroy, J.J., Kunin, W.E. and Edwards, D.P., 2016. How should beta-diversity inform biodiversity conservation?. Trends in ecology & evolution, 31(1), pp.67-80.

Soliveres S., Maestre F.T., Eldridge D.J., Delgado-Baquerizo M., Quero J.L., Bowker M.A., Gallardo A. 2014. Plant diversity and ecosystem multifunctionality peak at intermediate levels of woody cover in global drylands. Global Ecology and Biogeography **23**(12): 1408-1416.

Sørenson, T.A. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. Biologiske Skrifter Kongelige Danske Videnskabernes Selskab 5:1–34.

Strona, G., & Fattorini, S. (2014). On the methods to assess significance in nestedness analyses. *Theory in Biosciences*, *133*(3-4), 179-186.

Strona, G. and Fattorini, S. 2014. NeD. http://ecosoft.alwaysdata.net/

Sorrie, B.A. and Weakley, A.S. 2001. Coastal Plain vascular plant endemics. Castanea 66: 50-82.

The National Cohesive Wildland Fire Management Strategy: Phase III. Southeast Regional Action Plan. April 2013. http://www.forestsandrangelands.gov/strategy/Regional_Strategy_Committees/Southeast/index.shtml

Waller, S.S. and J. K. Lewis. 1979. Occurrence of C3 and C4 Photosynthetic Pathways in North American Grasses. Journal of Range Management 32: 12-28.

Wright, D.H. & Reeves, J.H. 1992. On the meaning and measurement of nestedness of species assemblages. Oecologia 92: 416.

Veldman J.W., Buisson E., Durigan G., Fernandes G.W., Le Stradic S., Mahy G., Negreiros D., Overbeck G.E., Veldman R.G., Zaloumis N.P., Putz F.E. 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. Frontiers in Ecology and the Environment 13(3): 154-162.

Vellend, M., Verheyen, K., Flinn, K.M., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., Graae, B.J., Bellemare, J., Honnay, O. and Brunet, J., 2007. Homogenization of forest plant communities and weakening of species–environment relationships via agricultural land use. Journal of Ecology, 95(3), pp.565-573.

Vittoz P. and Engler R. 2007. Seed dispersal distances: a typology based on dispersal modes and plant traits. Botanica Helvetica 117: 109–124.